Ellobiopsidae of Alaskan Coastal Waters

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ABSTRACT: Four species of ellobiopsids were taken in Alaskan coastal waters. *Thalassomyces fagei* (a synonym of *Amallocystis fagei*) was found to parasitize specimens of the euphausid *Thysanoessa raschii* taken in Kachemak Bay, Alaska. The development of *T. fagei* external to the host from a small knob to the mature form was found to occur by repeated dichotomous branching. *T. fagei* occurred during April and May but was not observed at other times of the year. *Thalassomyces* sp. was found to be parasitic on specimens of the mysid *Acanthomysis pseudomacropsis* taken in Kachemak Bay, Alaska. The range of *Thalassomyces capillosus,* parasitic on the caridean *Pasiphaea pacifica,* is extended from Coos Bay, Oregon, to Orca Bay, Prince William Sound, Alaska. *Ellobiopsis chattoni* was found to parasitize the copepod *Metridia longa,* a new host of this ellobiopsid. Specimens of *E. chattoni* were taken in the waters of southeastern Alaska, extending the range of *E. chattoni* from the Atlantic to the north Pacific.

THE SYSTEMATIC POSITION of the family Ellobiopsidae Coutière and the genera therein has been an enigma since their original description. According to Margaret Jepps (1937), T. Scott in 1897 first described the ellobiopsid now known as *Ellobiopsis chattoni* as a "? infusorian parasite" of the copepod *Calanus finmarchicus.* She states also that in 1910 Caullery associated the ellobiopsids with the Dinoflagellata. Various authors have continued to consider these organisms to be closely related to the dinoflagellates. Jepps points out that a relation with the fungi is possible. Boschma (1949, 1956, and 1959) reviewed the entire group and preferred to consider them as "Protista of uncertain position." He noted that the ellobiopsids have affinities with the following groups: parasitic peridinians, flagellates, and possibly fungi of the family Saprolegniaceae, and that the group is made up of a number of heterogeneous elements.

The family Ellobiopsidae is a rather heterogeneous group consisting of several genera. Members of the genus *Ellobiocystis* are epibionts, whereas members of the genera *Ellobiopsis* and *Thalassomyces* are parasites. This study is concerned only with the last two genera. Various pelagic crustaceans, including copepods, euphausids, and carideans, are hosts of species of *Ellobiopsis* and *Thalassomyces.*

Organisms of the genus *Ellobiopsis* parasitize several species of copepods. Various species of *Calanus* have been reported by Marshall et al. (1934), Marshall and Orr (1955), and Jepps (1937) to be parasitized by *Ellobiopsis chattoni. Pseudocalanus* (Marshall, 1949), *Clausocalanus* (Hovasse, 1951), *Acartia* (Boschma, 1956), and *Metridia,* in this work, have also been found as hosts of *E. chattoni.*

Jepps (1937) described very early forms of this parasite which she found on the antennae and mouth parts of *Calanus finmarchicus.* These first appeared as small knobs on the setae of the mouth parts. At maturity *E. chattoni* consists of a pear-shaped part, the trophomere, which is attached by a stalk to the host's appendage. Distal to the trophomere there may develop one or two rounded segments, the gonomeres, in which sporulation takes place. According to Jepp's description of sporulation in *E. chattoni,* small buds arise on the free surface of the gonomere, each of which undergoes a series of fissions, forming spores. The mechanism of spore release and the relation between free spores and the occurrence of small knobs on the host appendages is unknown.

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Species of *Thalassomyces* (formerly known as *Amallocystis*) are different in many respects from those of *Ellobiopsis*. Each *Thalassomyces* consists of a tuft of trophomeres extending from a central stalk, whereas each *Ellobiopsis* has only one trophomere. The number of trophomeres extending from the stalk is used as a species-differentiating character in *Thalassomyces*.

The gonomere (or gonomeres) which forms on the distal end of the trophomere is separated by a septum from the trophomere. Individuals of *Ellobiopsis* species have one or two gonomeres. If more than one gonomere is present, as in the *Thalassomyces* species and some *Ellobiopsis* species, each is separated from the next by a septum. Sporulation has not been described for any *Thalassomyces* species but is assumed to occur. Old individuals of *Thalassomyces* spp. may be found with numerous empty gonomeres; some with collapsed walls may remain attached to the trophomere.

Various euphausids, mysids, and carideans have been reported as hosts for *Thalassomyces* species. The ellobiopsid may be attached ventrally to the host's abdomen, as in *T. racemosus*, to the dorsal surface of the carapace, as in *T. fagei* and *Thalassomyces* sp., or at the base of the rostrum, as in *T. capillosus* (Boschma, 1956).

As a result of this study the ranges for three species of ellobiopsids have been extended to Alaskan waters. They are *T. fagei*, *T. capillosus*, and *E. chattoni*. *T. capillosus* is the only species of the three previously recorded in the north Pacific Ocean. The development of *T. fagei* is described, and seasonal distribution of this species is discussed. *Metridia longa* was found to be a host for *E. chattoni*.

OBSERVATIONS AND DISCUSSION

Thalassomyces fagei

The genus was named *Amallocystis* until 1959, when Boschma pointed out that, because of its priority, *Thalassomyces* is the valid name.

The euphausid *Thysanoessa raschii* (M. Sars) has been recorded as host for this ellobiopsid on two previous occasions. Einarsson (1945) described *Amallocystis* sp. parasitic on *T. raschii* taken in May in Faxafloi to the west of Iceland. Boschma (1949) established that the *Amallocystis* sp. of Einarsson was *A. fagei* (Boschma), and later (1959) he corrected the generic name to *Thalassomyces*. Glover (1952) observed two specimens of this euphausid infected with *T. fagei*. One was taken in July and the second in August of 1948 in the region of May Island in the Firth of Forth. Initially *T. fagei* (Boschma) was described as an Antarctic species, but its distribution has been extended to include the northern Atlantic waters by reports of Einarsson (1945), Glover (1952), and Macdonald (1927). Macdonald reported the occurrence of *Staphlocystis racemosus* on the euphausid *Meganyctiphanes norvegica* taken in the Clyde Sea. Boschma (1949) believes that this ellobiopsid was *T. fagei* and not *S. racemosus*.

In our investigation we also found *T. fagei* parasitic on *Thysanoessa raschii*. The specimens were taken during the spring of 1963 in three small inlets which are part of Kachemak Bay, Alaska (59°27′N, 151°33′W). The samples were taken in 20-minute oblique hauls of a ½-m plankton net with a standard No. 2 mesh. The depth in the area did not exceed 53 fathoms. This is the first record of this species of ellobiopsid from the Pacific Ocean, and its range is thus extended from the Atlantic to the northeastern Pacific.

The ellobiopsid parasites are attached to the host by a stalk which extends through the dorsal side of the carapace and penetrates the tissues below. The parasite is located in a dorsal concavity on the carapace of the host which is not found in uninfected euphausids (Fig. 1). An infected *T. raschii* usually bears only one *Thalassomyces*, although up to four were observed. A specimen bearing two parasites is shown in Figure 2.

The mature parasite has 30–50 trophomeres which are ramifications of the single central stalk. The trophomeres are expanded distally into a club shape. Trophomeres with one to six gonomeres were observed, although more commonly three to five occur. The gonomeres are spherical to slightly elliptical in shape. Figures 3 and 4*f* are a photograph and a camera lucida drawing respectively of a mature parasite. In older individuals some of the distal gonomeres are empty. The gonomere remnant may break

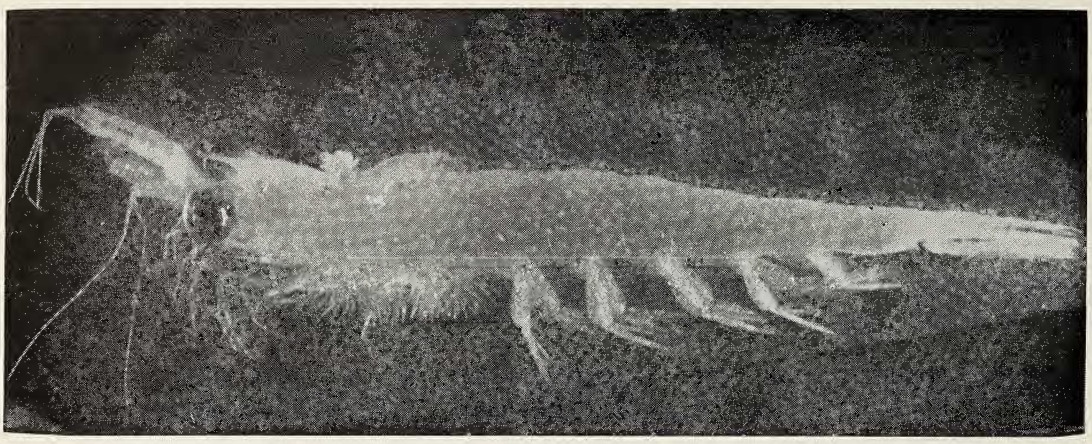

FIG. 1. A young ellobiopsid located in a concavity on the dorsal side of host's carapace.

off, leaving a small tuft, or the walls may collapse, producing a filament hanging from the end of a more proximal gonomere (Fig. 4*f*). Jepps (1937) has observed that in *Ellobiopsis chattoni,* parasitic on *Calanus finmarchicus,* this condition of the gonomere is the result of sporulation. She noted that when all the spores have been released, the test of the distal segment either degenerates or is left full of debris.

The development of *Thalassomyces fagei* was worked out from a sequence of specimens taken in various stages of growth (Fig. 4). The ellobiopsid was removed from its host and placed with the stalk extending upward to facilitate drawing. The illustrations show this aspect of the parasite, except Figures 4*a* and 4*b*, which are views from one side. All the drawings were done with the aid of a camera lucida.

It is not known whether the initial infection by the parasite is located internally or externally. Jepps (1937) hypothesized that *E. chattoni* initially penetrates the host from the outside. In the material of *Thysanoessa raschii* examined in the present study, *Thalassomyces fagei* was found to have a well-established internal structure at the earliest stages in its external development. Figure 4*b* is a lateral view of *T. fagei* shown extending through the host carapace. The structure in the lower left is the "sieve plate" of Boschma (1949). Numerous protoplasmic excrescences protrude through openings in the cuticle of the ellobiopsid. These excrescences are thought to be the organ of absorption of food for the parasite.

The major function of the external structure of the parasite is assumed to be reproductive.

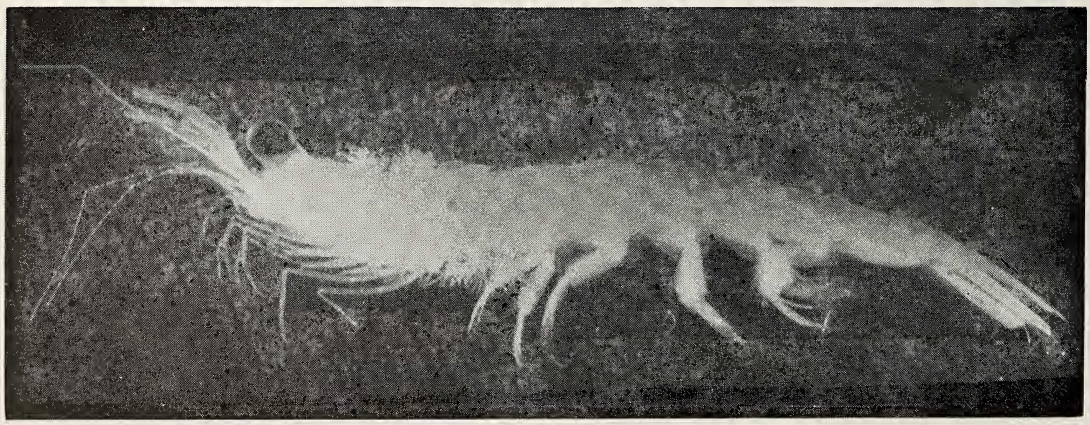

FIG. 2. Euphausid with two discrete parasites.

Whether reproduction is sexual or asexual is unknown. These observations agree with the hypothesis accepted by Boschma (1949) for *T. fagei* concerning the assumed release of spores from the gonomere. Jepps (1937) described sporulation in the distal structure which she termed the gonomere of *Ellobiopsis chattoni.* Hovasse (1951) observed sporulation of *E. fagei.* No observations of sporulation in a *Thalassomyces* species are available.

The external development of *T. fagei* is initiated by a small knob-shaped structure appearing through the middorsal region of the carapace of the host. This single knob bifurcates slightly, producing a bilateral structure (Fig. 4*a*). The next stage appears to be the result of simultaneous bifurcation of each of the previously formed lobes, resulting in a four-lobed structure (Fig. 4*c*). Further development of *T. fagei* is accomplished by repeated simultaneous dichotomous branching of each of the existing lobes. The simultaneous nature of the bifurcation is retained until the fifth or sixth division at which time the branching appears to get out of phase.

In this study 77 specimens of *T. fagei* were examined. These were taken in plankton samples from three stations located in the Cook Inlet area of Alaska. The locations of the stations were as follows: at the mouth of Kasitsna Bay (59° 28.7′N, 151°33′W) and two stations in Tutka Bay (59°26.5′N, 151°22.7′W, and 59°25.5′N, 151°19.5′W).

The seasonal distribution of *T. fagei* was found to coincide in part with that reported for the same species parasitic on *Thysanoessa inermis* by Einarsson (1945). He found *Thalassomyces fagei* (as *Amallocystis* sp.) on mature euphausids during May only. In our work during February and March of 1963 numerous *Thysanoessa raschii* were observed, but most of the individuals taken during this time were juveniles. Early stages of *Thalassomyces fagei* first appeared on the host early in April, 1963. Mature ellobiopsids were taken from late April until about the first of June. The external structures of *T. fagei* were not present on the euphausids taken in February or March, nor were they present late in June. During May, 1963 we noted 13% average infection of *Thysanoessa raschii* by *Thalassomyces fagei.* This was based on three samples containing 239 specimens of *Thysanoessa raschii,* of which 33 were parasitized.

It appears unlikely, at least from the preserved material, that a mature *Thalassomyces fagei* could pass through the hole in the carapace of the host at molting. This is due to the fact that the host's exoskeleton closely surrounds the stalk of the ellobiopsid. Since euphausids have a high intrinsic rate of molting, one can assume either that the euphausids continue to molt with their

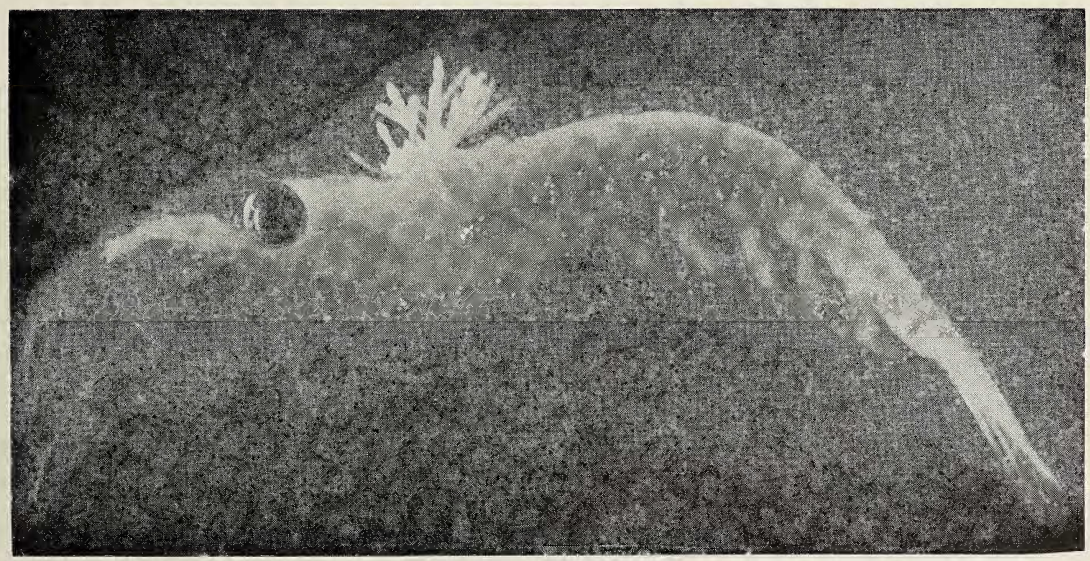

FIG. 3. Euphausid with a mature parasite.

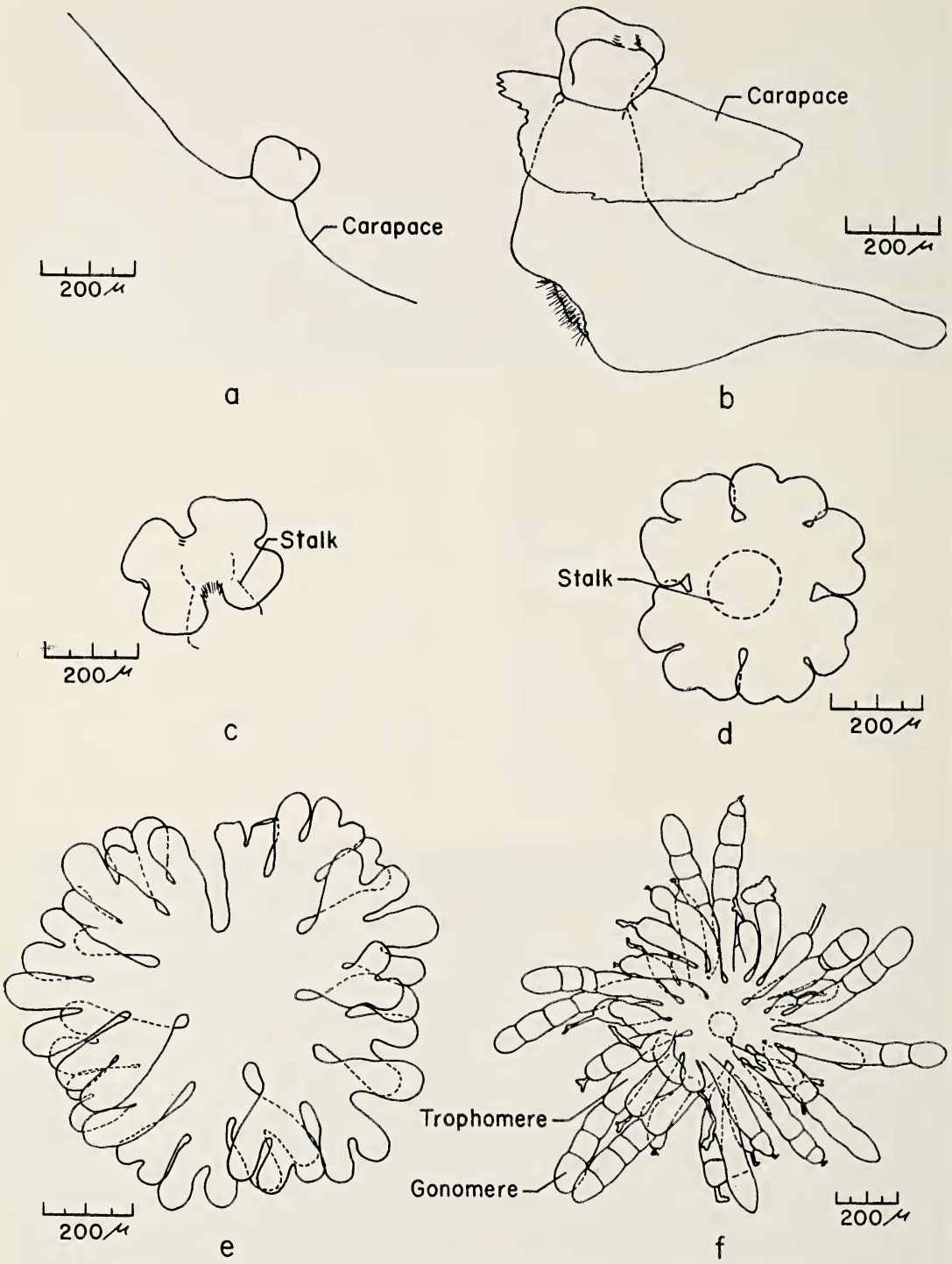

FIG. 4. Drawings illustrating the developmental stages of *Thalassomyces fagei*.

usual frequency or that the parasite interferes with the regulation of molting. In the former case, the external development of *T. fagei* during the intermolt would of necessity be extremely rapid. If the latter is true, as is the case with the rhizocephalans, molting would be held in abeyance while the external development and assumed reproduction of *T. fagei* take place.

In order to resolve this question and others, work on the internal development needs to be undertaken. Most studies on ellobiopsids, including this one, have dealt with the external aspects of these parasites only, while in reality it is the internal aspects which will reveal their biological status.

The observations on the effect of *Thalassomyces fagei* on *Thysanoessa raschii* agree with the reports of Einarsson (1945) on the effects of *T. fagei* on *Thysanoessa inermis*. Einarsson stated that *T. fagei* probably castrates the animal it attacks. None of the parasitized *Thysanoessa raschii* examined in this study had either the male antennal armature or the first pleopods developed as copulatory organs; in the case of females no sign of a thelycum was evident. Einarsson (1945) showed that parasitized mature females had completely disorganized ovaries through which ramifications of the stalk of the parasite extended.

Boschma (1949) sectioned parasitized euphausids and found that the ellobiopsid did not disorganize the host's ovary, although the protoplasmic excrescences which protrude through holes in the sieve plate extended throughout the organ. The ovary was not degenerated, although Boschma found that all the eggs present were small.

The most complete works on the genus *Thalassomyces* are those by Boschma (1949 and 1959), which contain a comprehensive review of the literature as well as descriptions of the species.

On the basis of these and other observations concerning the biology of ellobiopsids, a number of conclusions and hypotheses can be drawn concerning members of the genus *Thalassomyces*.

1. The development of the structures external to the euphausid and the similarity of these to reproductive structures of *Ellobiopsis* strongly suggest that they are primarily reproductive. These external structures follow the establishment of a large internal body thought to be of a vegetative nature. The length of "life" of the internal portion of the parasite and its seasonal presence are unknown. Therefore the true percentage infection cannot be determined on the basis of the external structures alone.

2. The external reproductive structures of *T. fagei* appear in early summer in Alaska, whereas they appear in midsummer in the Atlantic. The duration of this manifestation of individual ellobiopsids is unknown.

3. Our observations in this study and those of Einarsson and Boschma on the sexual development of euphausids support the interpretation that *T. fagei* suppresses the sexual development of the host. Also the ellobiopsid may interfere with the endocrine control of molting, at least during its period of external development.

4. Further understanding of the biological effects of these parasites on planktonic crustaceans will be achieved only by laboratory investigations on the internal development of the parasite and on the nature and fate of the bodies produced in the gonomere.

Thalassomyces sp.

Six specimens of *Thalassomyces* sp. were found to parasitize the mysid *Acanthomysis pseudomacropsis*. The ellobiopsid is generally located on the dorsal surface of the carapace of the mysid. In each case the mysid was parasitized by two ellobiopsids. In one instance, one of the ellobiopsids was located on the carapace, and the other was on the dorsal surface of the sixth abdominal segment of the mysid. The mature *Thalassomyces* specimens were taken in plankton samples from stations in the Kachemak Bay area of Alaska (59°27′N, 151°33′W) in October and December, 1963 and in February, 1964.

The mature parasite has 7–20 short-stalked trophomeres which are ramifications of the single central stalk. The trophomeres average 0.75 mm long, although this feature is variable. The usual number of gonomeres present on each trophomere is three, and no more than this num-

ber have been observed. The transverse diameter of the gonomeres ranges from 0.14 to 0.21 mm, the average being 0.17 mm.

The species identification of these specimens has not been determined. This ellobiopsid may be *T. fagei,* although there are differences in a number of external features of *Thalassomyces* sp. from the specimens of *T. fagei* parasitic on the euphausid *Thysanoessa raschii* taken in the same area. The number of trophomeres, the length of the trophomere stalk, and the number of gonomeres vary from the previously mentioned species. Boschma (1959) pointed out that a number of variations of this type occur among *T. fagei* individuals parasitic on different species of euphausids. The location of the ellobiopsid on the carapace tends to support the hypothesis that this is *T. fagei,* while the fact that this species parasitizes a mysid rather than a euphausid may be sufficient to propose this as a new species, inasmuch as *T. fagei* has only euphausid hosts. The only *Thalassomyces* species reported to parasitize a mysid is *T. fasciatus.* This ellobiopsid is located on the ventral side of the first abdominal segment of its host.

Until more material is available and can be examined by an authority, it is advisable to consider this ellobiopsid as *Thalassomyces* sp.

Thalassomyces capillosus

The first report of ellobiopsids from the northern and eastern Pacific was that of McCauley (1962). He found *Thalassomyces capillosus* (Fage), formerly known as *Amallocystis capillosus,* on a specimen of *Pasiphaea pacifica* Rathbun, a pelagic shrimp taken 15 miles west of Coos Bay, Oregon (43°20.4′N, 124°45.8′ W) in a midwater trawl. McCauley (1962) stated, "This work adds *P. pacifica* as a host and extends the known range of this parasite to the northeastern Pacific." According to McCauley, *T. capillosus* had previously been described as parasitic on several species of pasiphaeid shrimp, most of which were taken in the north Atlantic.

Five *Pasiphaea pacifica* taken by the Exploratory Fishing and Gear Research Base of the Bureau of Commercial Fisheries, Juneau, Alaska, were examined for ellobiopsids. A single specimen of *P. pacifica* taken by a shrimp trawl at station No. 427 located in Orca Bay, Prince William Sound, Alaska (60°34′N, 146°01′W) was parasitized. This individual was taken between depths of 74 and 120 fathoms on September 9, 1962, by Rathjen (1963). In addition, a single specimen taken in Lynn Canal in southeastern Alaska (58°51.2′ N, 135°15.5′W) was parasitized by *T. capillosus.* This pasiphaeid was taken May 14, 1964, by an Isaac-Kidd midwater trawl at a depth of 59.6 fathoms.

The ellobiopsid is located dorsal to the eyes of the host at the base of the rostrum. On one specimen there were approximately 40–50 trophomeres on either side of the rostrum; on the other specimen there were 50–60. This estimation of the number of trophomeres on the first may not be accurate because the specimen was in poor condition. Distal to the trophomere of the parasite is one or, more commonly, two gonomeres. The terminal gonomere is ovoid, almost twice as long as broad. When two gonomeres are present, the proximal one is somewhat rectangular because of the septa which separate it from the more distal gonomere and from the trophomere.

The morphology of the parasite, its size and location on the host, and the host species agree for the most part with the description of *T. capillosus* (Fage). The only discrepancy was that rather than a single gonomere there were almost always two gonomeres on each trophomere.

Effects of *T. capillosus* on the carapace of *P. pacifica* similar to those found by McCauley were noted. The rostrum is distorted and projects almost dorsad rather than anteriad. On either side of the base of the rostrum is a swelling not found in unparasitized *P. pacifica.* A dumbbell-shaped opening in the carapace extends between the two swellings. A tuft of trophomeres of *T. capillosus* extends from the tissue of the host through both of the expanded ends of the slit. Figure 5 is a camera lucida drawing illustrating the rostrum of a parasitized *P. pacifica.*

This study extends the known range of *T. capillosus* as a parasite on *Pasiphaea pacifica* from off the Oregon coast (McCauley, 1962) to the Prince William Sound area of Alaska. It is expected that further observations will fill in the range and possibly extend it still farther.

Ellobiopsis chattoni

The genus *Ellobiopsis* contains two species, *E. fagei* Hovasse and *E. chattoni* Caullery. *E. fagei* was described as parasitic on the copepod *Clausocalanus arcuicornis* Dana by Hovasse (1951). *E. chattoni* is known to be parasitic on the following copepods: *Calanus finmarchicus* (Marshall et al., 1934; Marshall and Orr, 1955; Jepps, 1937); *Calanus helgolandicus* (Boschma, 1949); *Pseudocalanus minutus* (Marshall, 1949); and *Acartia clausii* (Boschma, 1956). Marshall et al. and Marshall and Orr state that *E. chattoni* is more common on *Calanus* during the summer than the winter.

In our investigation *Metridia longa* was found to be a host for *Ellobiopsis chattoni.* This is the first record of a species of *Metridia* as host for ellobiopsids. *M. lucens,* which was present in the same samples, was not found to be parasitized by *E. chattoni.* Parasites were observed only on Stage V males and females. *M. longa* was the only copepod taken which was host to a species of ellobiopsid.

The plankton samples examined during this study were taken in southeastern Alaska at the mouth of Auke Bay (58°21'N, 134°41'W) by the Oceanography Investigation of the Bureau of Commercial Fisheries Biological Laboratory, Auke Bay, Alaska. The samples were taken monthly during 1962 and 1963. Samples were taken both during the day and at night. *Metridia longa* and *M. lucens* were the most abundant copepods in the Auke Bay samples taken during the late fall in both 1962 and 1963. Throughout the other seasons *Metridia* are taken in considerably fewer numbers. At night both species of *Metridia* are common in the sample taken just beneath the surface, whereas in the daytime *Metridia* are most common in the samples taken from approximately 20 m. Few *Metridia* were taken in the samples from Kasitsna Bay, Alaska, and none of these were parasitized by *E. chattoni.*

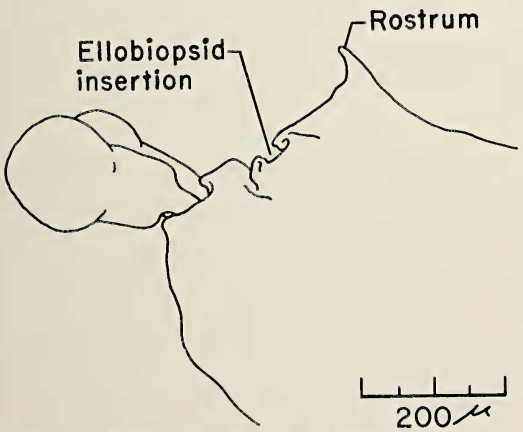

FIG. 5. Drawing showing the anterior portion of the carapace of an infected *Pasiphaea pacifica.*

E. chattoni was most abundant in the samples from Auke Bay taken in October and November of 1962 and 1963. The percentage of infection was established by examining 250 specimens of *Metridia* and calculating the percentage of infection in this subsample. Samples taken in the middle of November, 1962 showed the highest infection rate. The percentage of infected copepods ranged from 7.7% in the daytime samples to 22.4% in the nighttime samples taken at the same station. No explanation of this difference is available. During October and November, 1963 approximately 5% of the *Metridia* specimens were found to be parasitized by *E. chattoni.*

The morphology and development of *E. chattoni* is described and discussed by Jepps (1937). Our observations of *E. chattoni* on *Metridia* agree with those reported by Jepps on its parasitizing *Calanus finmarchicus.* An ellobiopsid individual initially appears as a small knoblike structure on one of the setae of any of the cephalic appendages. The mature individuals are attached by a stalk which extends into the tissue of the host's appendage. There are one or two gonomeres present on the mature ellobiopsid. The distal gonomere sometimes has an "apical cone" as described by Jepps. Although several immature *E. chattoni* may be located on a single host, no more than three mature parasites were observed on any single specimen of *M. longa.*

The finding of *Ellobiopsis chattoni* on *Metridia longa* in the coastal waters of southeastern Alaska extends the known range of this parasite from the northern Atlantic Ocean to the northeastern Pacific Ocean. This is the first report of *E. chattoni* taken in the Pacific.

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